

Cyprinus-like pharyngeal bones and teeth (Teleostei, Cypriniformes, Cyprinidae) from the Early–Middle Oligocene deposits of South China

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Abstract Here we describe †*Nanningocyprinus wui* gen. et sp. nov, a fossil *Cyprinus*-like fish from the Early-Middle Oligocene deposits of Langdong, Nanning Basin, Guangxi Province, South China. †*Nanningocyprinus wui* is represented by a number of pharyngeal bones and teeth. It differs from all other cyprinid fishes in the following character combination: tooth formula —3·2·1, crushing molar-like A1 much larger than A2, only one groove on the grinding surface of A2 and B1 respectively, and the anterior angle of the pharyngeal bone triangular and prominent. The new-found *Cyprinus*-like fish, along with the previously known Late Eocene †*Eoprocypis maomingensis* (*Procypis*-like) and Oligocene †*Huashancyprinus robustispinus* (*Cyprinus*-like) from South China, further indicates an early branching and diversification of the Cyprininae (Cyprinidae) in this area.

Key words Nanning Basin; Yongning Formation, Oligocene; Cyprinidae, pharyngeal bone and teeth

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Many disarticulated bones of fishes and reptiles have been found from Early-Middle Oligocene deposits in Langdong, Nanning Basin, Guangxi, South China since 2000 (Chen et al., 2015a). Among them, some are the pharyngeal bones (enlarged fifth ceratobranchial) and teeth of a *Cyprinus*-like fish. Though fishes of *Cyprinus*, a genus of Cyprinidae that contains Asian Common Carp, are very common in the present freshwater fauna, little is known about their early evolution. Only one genus with one species †*Huashancyprinus robustispinus*, which closely related to *Cyprinus*, have been found from the Paleogene (Chen and Chang, 2011). Therefore, the following description of new fossil materials of *Cyprinus*-like fish is in need to further understanding of the morphology, diversification, distribution, and evolution

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of the *Cyprinus*, and even the family Cyprinidae, which is the most diversified and speciose freshwater fish group (Nelson et al, 2016).

1 Materials and methods

Fossil materials studied in this paper were collected from the Early–Middle Oligocene deposits in Langdong, Nanning, Guangxi, China, and are deposited in the collection of the Natural History Museum of Guangxi Zhuang Autonomous Region (NHMG) with catalog numbers NHMG 033663–033672. The terminology of the pharyngeal bone and teeth is mainly based on Chu (1935). Tooth positions in the adult dentition are numbered according to Nakajima (1984). The most medial row is named main row (or row A), and lateral rows named outer and most-outer rows (or rows B and C). Tooth position is numbered from anterior to posterior in each row. So, A1, A2, and A3 represent the first, second, and third tooth of the main row (row A), whereas B1 and C1 represent the first tooth of row B and row C respectively, and so on. Each tooth consists of a enameloid-coated crown and a dentine/ predentine-only neck region, which terms were used in Sytchevskaya (1989). The tooth base at the proximal end of a pharyngeal tooth is ankylosed to a depression on pharyngeal bone (tooth-base pit). The dagger symbol “†” is used to denote extinct taxon.

2 Systematic paleontology

Superorder Ostariophysi Sagemehl, 1885

Order Cypriniformes Bleeker, 1860

Family Cyprinidae Bonaparte, 1840

Subfamily Cyprininae *sensu* Cavender & Coburn, 1992

Tribe Cyprinini *sensu* Yang et al., 2010

†*Nanningocyprinus* gen. nov.

Etymology Nanning, name of the locality where the specimens were collected; *cyprinus*, genus name for carp, Latin.

Type species †*Nanningocyprinus wui* gen. et sp. nov.

Diagnosis Same as for the type and only known species.

†*Nanningocyprinus wui* gen. et sp. nov.

(Fig. 1)

Etymology The species name is dedicated to the late Prof. Hsianwen Wu, who made great contributions to the study of Chinese cyprinids.

Holotype NHMG 033663 (Fig. 1a–b), a nearly complete right pharyngeal bone with pharyngeal teeth A1, A2 and B1.

Paratype NHMG 033665 (Fig. 1e), a nearly complete left pharyngeal bone with pharyngeal teeth A1 and B1.

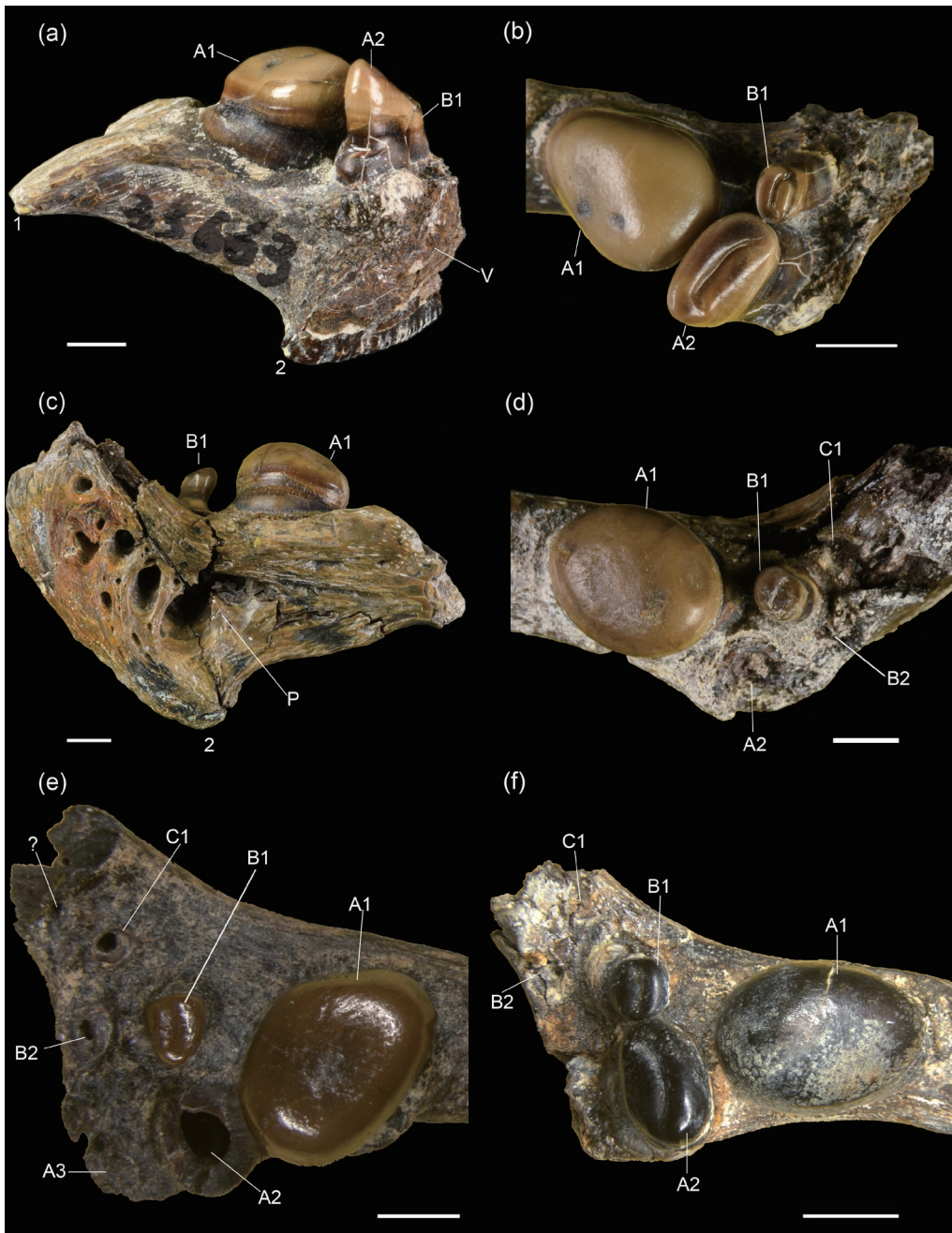


Fig. 1 pharyngeal bone and teeth of †*Nanningocyprinus wui* gen. et sp. nov.

NHMG 033663: (a) ventro-lateral view, (b) dentigerous surface view;

NHMG 033664: (c) pitted surface view, (d) dentigerous surface view;

NHMG 033665: (e) dentigerous surface view; NHMG 033667: (f) dentigerous surface view

Abbreviations: 1. tip of anterior limb; 2. anterior angle; P. pitted surface of pharyngeal bone;

V. ventral surface of pharyngeal bone. Question mark indicates an uncertain structure that is a tooth-base pit near C1. All scale bars except (e) equal to 3 mm, scale bar of (e) equals to 1 mm

Referred materials NHMG 033664 (Fig. 1c–d), an incomplete right pharyngeal bone with pharyngeal teeth A1 and B1; NHMG 033666, an incomplete left pharyngeal bone with pharyngeal teeth A1 and A2; NHMG 033667 (Fig. 1f), an incomplete left pharyngeal bone with pharyngeal teeth A1, A2, and B1; and NHMG 033668–033672, incomplete pharyngeal bones with pharyngeal tooth A1.

Locality and horizon Langdong, Nanning, Guangxi. Lower–Middle Oligocene, lower part of Yongning Formation.

Diagnosis Dental formula $—3 \cdot 2 \cdot 1$, teeth molar-like, A1 about three to four times of A2 in size, A2 and B1 with only one transverse groove on the grinding surface.

Description The overall appearance of the pharyngeal bone and teeth resembles that of the fishes in the genus *Cyprinus*. The pharyngeal bone is relatively broad and bending in the middle (NHMG 033663–033665). Its anterior limb is short. The surface ventral to the teeth is comparatively wide. The anterior angle is triangular and prominent, opposite to the anterior margin of A2. The anterior edentulous process is broad at the base and pointed at the tip. The pitted surface is wide and extending forward to the anterior limb. There are some foramina on the pitted surface via which nerves and blood vessels passing through (Fig. 1a, c). The dentigerous surface is moderately broad with three rows of teeth on it (Fig. 1d–f).

Two rows of pharyngeal teeth, including A1, A2, and B1, were preserved in the holotype (Fig. 1b). The shape of all preserved teeth is molar-like. The teeth in the row A are much larger than that in the row B. A1 is the largest tooth with its grinding surface smooth and slightly convex. A2 is much smaller than A1, with its size about 1/3 of the latter. The length of A2 (distance in antero-posterior direction) is about half of its width (distance in mesio-lateral direction). On the grinding surface of A2, there is a transversal groove. B1 is much narrower and shorter than A2, with the length slightly shorter than the width of itself. On its grinding surface, there is a groove extending mesio-laterally as in A2. The above shape and size pattern of A1, A2, and B1 are consistently seen in all specimens, except that B1 of the holotype is somewhat compressed instead of cylindrical in the rest specimens.

The pharyngeal dental formula is $—3 \cdot 2 \cdot 1$, recognized from NHMG 033664–033667 (Fig. 1d–f). Three large teeth, A1, A2, and B1, are generally well-preserved in all specimens. The crown of A3, B2, and C1 are usually missing, whereas fragmentary tooth necks/bases and/or tooth-base pits are clearly visible.

3 Discussion and conclusion

3.1 Taxonomic position of the new form

The character combination of pharyngeal bone and teeth possessed by the new form †*Nanningocyprinus*, that three rows molar-like pharyngeal teeth with groove on the grinding surface except A1, are only seen in cyprinid fishes that belong to the genus *Cyprinus* Linnaeus, 1758 or †*Huashancyprinus* Chen & Chang, 2011 prior to this study. Although †*Nanningocyprinus* resembles *Cyprinus* and †*Huashancyprinus* in having three rows of molar-

like pharyngeal teeth, the pharyngeal tooth formula $—3·2·1$ of †*Nanningocyprinus* differs from that of *Cyprinus* and †*Huashancyprinus* ($—3·1·1$). The intraspecific variations in the pharyngeal tooth formulae in some cyprinid fishes have been noted, however, the percentage of the variations of pharyngeal tooth formula $1·1·3—3·1·1$ is significantly low. In the case of the study of *Cyprinus carpio* conducted by Eastman and Underhill (1973), two teeth on the row B is only 3.7% based on the observation of 380 pharyngeal bones with teeth. In the rest species of *Cyprinus*, as far as the available references are concerned, no tooth of B2 has been reported (Chen and Huang, 1977; Wang, 1979; Zhou and Chu, 1986; Luo and Yue, 2000; etc). In our sampled specimens, all three pharyngeal bones, preserved with the portion that B2 can be possibly ankylosed to, are observed with either tooth neck or tooth-base pit, and thus confirm the $—3·2·1$ formula. If there is any intraspecific variation have occurred in †*Nanningocyprinus* resembling that of extant cyprinids addressed by Eastman and Underhill (1973), the variation won't significantly affect the recognition of the pharyngeal dental formula. Therefore, the pharyngeal tooth formula $—3·2·1$ of †*Nanningocyprinus* is distinguishable from that of *Cyprinus* and †*Huashancyprinus* ($—3·1·1$).

†*Nanningocyprinus* also differs from *Cyprinus* and †*Huashancyprinus* in the tooth size, shape, and tooth positions. First, A1 is much larger than A2, with its size about three to four times to that of A2 in †*Nanningocyprinus* (Fig. 1), whereas A1 is usually slightly larger or even smaller than A2 in all known extant (Chen and Huang, 1977; Zhou and Chu, 1986; Luo and Yue, 2000; Chen and Chang, 2011:fig. 5e–f) and certain fossil *Cyprinus* (Lee, 2004:fig. 3). In some fossil *Cyprinus*-like fish, A1 is about 1.5 times of A2 in size (Liu, 1985:fig. 1; Nakajima and Hattori, 1992:figs. 1–2); and in some others, such as †*Huashancyprinus*, A1 is slightly larger than A2 (Chen and Chang, 2011:fig. 5b). Second, the lateral wall of the crown of A2 in the new form is smooth as in *Cyprinus*, whereas †*Huashancyprinus* bears a number of deep grooves on the lateral wall of the crown. Third, the new form has only one groove on the grinding surface of A2 and B1 resembling the species that referred to “*C. (Mesocyprinus)*” by Luo and Yue in 2000, whereas the species referred to “*C. (Cyprinus)*” by Luo and Yue in 2000 have at least two grooves on the grinding surface of A2 and B1. Last, for the pharyngeal bone, there are variations in the development on the anterior angle among the species of *Cyprinus*. It is triangle and prominent in the new form, as in that of *C. carpio* (a “*C. (Cyprinus)*” species) (Pasco-Viel et al., 2010:fig. 3F) and †*Huashancyprinus*, but it is round in *C. fuxianensis* (Chen and Chang, 2011:fig. 5d), a so-called “*C. (Mesocyprinus)*” species. A summary of comparison on †*Nanningocyprinus wui* with *Cyprinus fuxianensis*, *C. carpio*, and †*Huashancyprinus* can be found in Table 1. To sum up, the new form is apparently different from any species of genus *Cyprinus* and †*Huashancyprinus*, and should be assigned to a new genus and species.

3.2 Distribution of *Cyprinus* and *Cyprinus*-like fishes and its implication

The Common Carp *Cyprinus carpio* presents disjunct distribution in Europe and East Asia, whereas all other species of the genus *Cyprinus* are restricted in East Asia, especially in the lakes of Yunnan Province and Xijiang River of Guangxi Province, South China (Bănărescu

Table 1 Comparison of †*Nanningocyprinus wui* with *Cyprinus fuxianensis*, *C. carpio*, and †*Huashancyprinus robustispinus*

	† <i>Nanningocyprinus wui</i>	<i>Cyprinus fuxianensis</i>	<i>Cyprinus carpio</i>	† <i>Huashancyprinus robustispinus</i>
Tooth formular	1·2·3—3·2·1	1·1·3—3·1·1	1·1·3—3·1·1	1·1·3—3·1·1
Size of A1 and A2	A1 about 3–4 times of A2	about equal	about equal	about equal
Number of groove on the grinding surface of A2	one	usually one, occasionally two	at least two	one
Number of groove on the grinding surface of B1	one	one	at least two	unknown
Anterior angle	triangle, prominent	round	triangle, prominent	triangle, prominent

1992; Chen and Huang, 1977). To date, a number of Neogene *Cyprinus* have been unearthed from the deposits of the Middle–Late Miocene to Pleistocene of China (Liu and Su, 1962; Liu, 1985; Tao and Hu, 2001; Chang and Chen, 2008), South Korea (Lee, 2004), Japan (Nakajima, 1985; Nakajima and Hattori, 1992; Nakajima and Yue, 1995; Nakajima et al., 2001; Yasuno, 1986, 2003), Mongolia (Sytchevskaya, 1989), Russian Altai (Sytchevskaya, 1989), and India (Kotlia, 1985) (Fig. 2). In Europe, *Cyprinus carpio* remains were found from a number of Pleistocene and Paleolithic localities along the valley of the lower reach of the River Don in Russia (Lebedev, 1960) (Fig. 2). Recently, Kovalchuk (2013) overviewed *Cyprinus* fossils from Late Miocene to Holocene of several localities of Ukraine, and Gaudant et al. (2014) described *Cyprinus* sp. from the Middle to Upper Miocene deposits in southern Spain (Fig. 2). It is interesting to note that some pharyngeal teeth with one groove on the grinding surface, similar to those of the living species *C. fuxianensis* and *C. yilongensis*, have been discovered from Nei Mongol (China) and Japan, which are completely outside of the distribution range of these living species. Also, those *Cyprinus* fossils from Spain, Mongolia, Altai (Russia), and India are not overlapped with the natural distribution of extant species of *Cyprinus*. No species of *Cyprinus* has been found from the deposits with age earlier than the Early Miocene. As for the *Cyprinus*-like fishes from the Paleogene, two single species based genera, †*Nanningocyprinus* and †*Huashancyprinus*, have been recovered from the Oligocene of Guangxi, South China. And these two fishes bear pharyngeal teeth with only one groove on the grinding surface resembling that of the foresaid Neogene *Cyprinus* and living species of *C. fuxianensis* and *C. yilongensis*.

Not only fossil species of *Cyprinus* or *Cyprinus*-like cyprinids, the Paleogene Cyprinini (*sensu* Yang et al., 2010) fish, †*Eoprocypis* (*Procypis*-like), is also unearthed from South China (Chen et al., 2015b). With all known fossil *Cyprinus* and the forms closely related to it allow us to draw a conclusion: Cyprinini have been present in East Asia at least since the Late Eocene, and South China might be the center of origin and diversification of this group; the Cyprinini has already diverged obviously during the Oligocene, and molariform dental morphotype, especially those with one groove on the grinding surface, is probably a plesiomorphic pharyngeal tooth type in cyprinids; and *Cyprinus* and the forms closely related to it were widespread in Eurasia and had a much wider distribution during the Neogene than

today. The absence of *Cyprinus*-like fish in most part of central Asia and South Asia of extant freshwater aquatic ecosystem is probably caused by the Cenozoic mountain-building activities in this area resembling that of *Cobitis* (Chen et al., 2010).

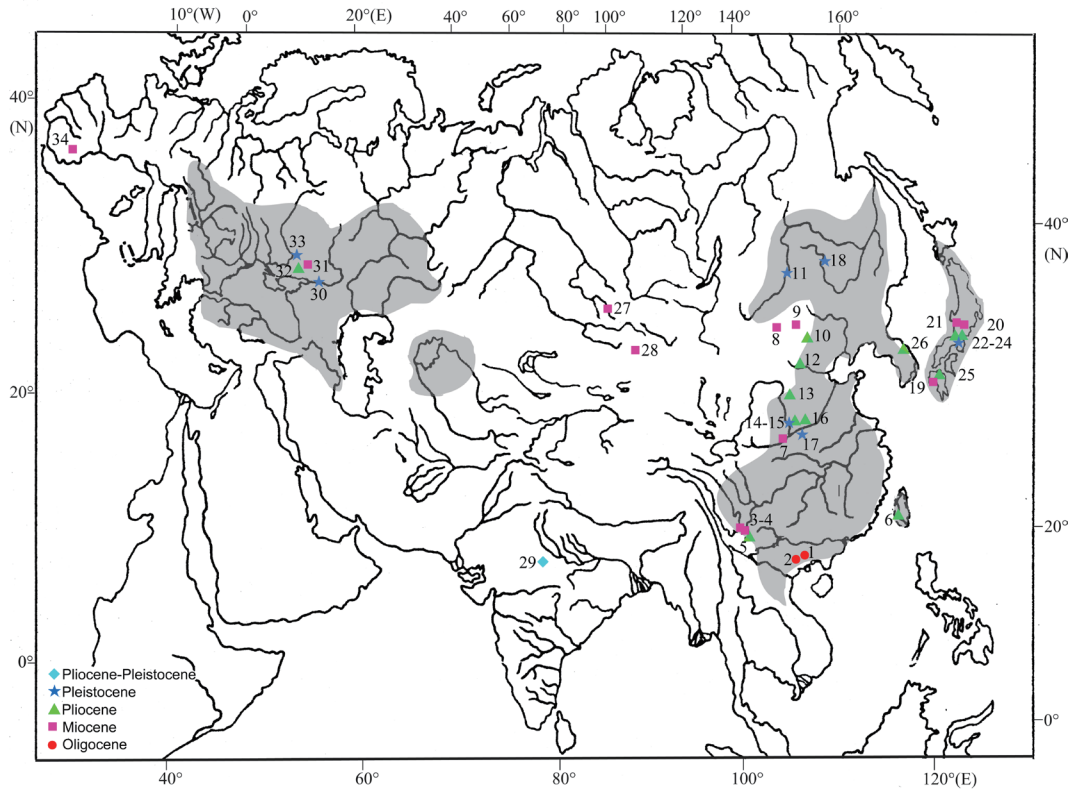


Fig. 2 Main localities of fossil *Cyprinus* and *Cyprinus*-like and distribution of the Recent *Cyprinus* (shaded) (based on Bănărescu, 1990:fig. 2/26)

1. Nanning, 2. Ningming, Guangxi; 3, 4. Yuanmou and Lufeng, 5. Yiliang, Yunnan; 6. Tainan, Taiwan;
7. Lantian, Shaanxi; 8. Tonggur, 9. Abagaqi, 10. Bilike, 11. Zhalainguoer, Nei Mongol; 12. Yangyuan, Hebei;
13. Yushe, 14, 15. Xianfeng, 16. Tangying, Shanxi; 17. Sanmenxia, Henan; 18. Fuyu, Heilongjiang, China;
19. Gifu, 20. Hyogo, 21, 22. Shiga, 23. Mie, Honshu; 24. Oita, 25. Matsuura City, Nagasaki, Kyushu, Japan;
26. Bukpyeong Basin, South Korea; 27. Russian Altai; 28. Shargain Gobi, Mongolia; 29. Karewa intermontane basin, Kashmir, northwestern India; 30. lower reach of the River Don, Russia; 31. Zaporizhia region,
32. Kherson region, 33. Poltava region, Ukraine; 34. southern Spain

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广西南宁渐新世基于咽齿的鲤亚科一新属

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摘要: 记述了产自广西南宁盆地渐新世早—中期的鲤科鲤亚科一新属种——伍氏南宁鲤 (†*Nanningocyprinus wui* gen. et sp. nov)。化石材料包括一些咽喉骨和咽齿。这些咽喉骨和咽齿的以下特征组合明显不同于其他鲤科鱼类: 齿式—3·2·1, 主行第一枚咽齿大小是第二枚的3~4倍, 第二枚咽齿及第二行第一枚咽齿咀嚼面上各仅有一条沟纹, 咽骨前角很发育。该属种的发现进一步证明鲤亚科是鲤科中较早的分支, 中国南方很有可能是鲤亚科的起源和分化中心。

关键词: 广西南宁盆地, 邕宁组, 渐新世, 鲤属, 咽骨及咽齿

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References

- Bănărescu P, 1990. Zoogeography of Freshwaters. Vol. 1. General Distribution and Dispersal of Freshwater Animals. Wiesbaden: AULA Verlag. 48–170, 499–510
- Bănărescu P, 1992. Zoogeography of Freshwaters. Vol. 2. Distribution and Dispersal of Freshwater Animals in North America and Eurasia. Wiesbaden: AULA Verlag. 524–531, 860–1091
- Chang M M, Chen G J, 2008. Fossil Cypriniformes from China and its adjacent areas and their palaeobiogeographical implications. Geol Soc Spec Publ, 295: 337–350
- Chen G J, Chang M M, 2011. A new early cyprinid from Oligocene of South China. Sci China Earth Sci, 54(4): 481–492
- Chen G J, Chang M M, Wang Q, 2010. Redescription of †*Cobitis longipectoralis* Zhou, 1992 (Cypriniformes: Cobitidae) from late Early Miocene of East China. Sci China Earth Sci, 53(7): 933–1090
- Chen G J, Liao W, Lei X Q, 2015a. First fossil cobitid (Teleostei: Cypriniformes) from Early-Middle Oligocene deposits of South China. Vert Palasiat, 53: 153–163
- Chen G J, Chang M M, Liu H Z, 2015b. Revision of *Cyprinus maomingensis* Liu, 1957 and the first discovery of *Procypris*-like cyprinid (Teleostei, Pisces) from the Late Eocene of South China. Sci China Earth Sci, 2015, 58(7): 1123–1132. doi: 10.1007/s11430-015-5085-7
- Chen X L, Huang H J, 1977. Cyprininae. In: Wu X W et al. eds. The Cyprinoid Fishes of China, Vol. 2. Shanghai: Shanghai People's Press. 395–438
- Chu Y T, 1935. Comparative studies on the scales and on the pharyngeals and their teeth in Chinese cyprinids, with particular reference to taxonomy and evolution. Biol Bull St John's Univ, 2: 1–290

- Eastman J T, Underhill J C, 1973. Intraspecific variation in the pharyngeal tooth formulae of some cyprinid fishes. *Copeia*, (1): 45–53
- Gaudant J, García-Alix A, Freudenthal M, 2014. Occurrence of pharyngeal teeth of the carp, *Cyprinus* Linnaeus (Teleostei, Cyprinidae) in the Middle and Upper Miocene of Andalusia (southern Spain): a puzzling disconnected palaeobiogeographical distribution. *C R Palevol*, 14: 25–29
- Kotlia B S, 1985. Vertebrate fossils and palaeoenvironment of the Karewa Intermontane Basin, Kashmir, northwestern India. *Curr Sci*, 54: 1275–1277
- Kovalchuk O M, 2013. History of the fossil carp fishes (Teleostei, Cyprinidae) in Ukraine. *Acta Zool Cracov*, 56(1): 41–51
- Lebedev V D, 1960. Quaternary Freshwater Ichthyofauna of European Part of USSR. Moscow: Moscow University Press. 1–402
- Lee Y N, 2004. The first cyprinid fish and small mammal fossils from the Korean Peninsula. *J Vert Paleont*, 24: 489–493
- Liu H T, Su T T, 1962. Pliocene fishes from Yushe Basin, Shansi. *Vert PalAsiat*, 6: 1–25
- Liu X T, 1985. Fish fossils from the hominoids bearing locality at Shihuiba, Lufeng, Yunnan. *Acta Anthropol Sin*, 4: 109–112
- Luo Y L, Yue P Q, 2000. Cyprininae. In: Yue P Q et al. eds. *Fauna Sinica, Osteichthyes, Cypriniformes III*. Beijing: Science Press. 91–433, 619–623
- Nakajima T, 1984. Larval vs. adult pharyngeal dentition in some Japanese cyprinid fishes. *J Dent Res*, 63: 1140–1146
- Nakajima T, 1985. Fossil pharyngeal teeth of cyprinids from the Pliocene Iga Formation of the Kobiwako Group at Ohyamada-mura, Mie Prefecture, Central Japan. *Assoc Geol Collaborat Jpn*, 29: 65–70
- Nakajima T, Hattori N, 1992. A new species of the cyprinid fish, *Cyprinus (Cyprinus) stridentatus*, from the Pleistocene Katata Formation of the Kobiwako Group in Otsu City, Shiga Prefecture, central Japan. *Earth Sci*, 46: 235–240
- Nakajima T, Yue P Q, 1995. A new species of the fossil cyprinid fish, *Cyprinus (Mesocyprinus) okuyamai*, from the Pliocene Ueno Formation of the Kobiwako Group in the Ueno Basin, Mie Prefecture, central Japan. *Earth Sci*, 49: 221–226
- Nakajima T, Matsuoka K, Kitabayashi E, 2001. Pharyngeal teeth of cyprinid fishes from Plio-Pleistocene Koitsuma Formation in Oita Prefecture, central Kyushu, Japan. *Earth Sci*, 55: 3–10
- Nelson J S, Grande T C, Wilson M V H, 2016. *Fishes of the World*. 5th ed. New Jersey: John Wiley & Sons Inc. 1–752
- Pasco-Viel E, Charles C, Chevret P et al., 2010. Evolutionary trends of the pharyngeal dentition in Cypriniformes (Actinopterygii: Ostariophysi). *PLoS ONE*, 5(6): e11293, doi:10.1371/journal.pone.0011293
- Sytchevskaya E K, 1989. Neogene freshwater fish fauna of Mongolia. *Joint Soviet-Mongol Paleontol Exped*, 39: 77–82
- Tao H J, Hu C H, 2001. Cyprinidae fossil fishes of Tainan Hsien, Taiwan. *Geology*, 21: 51–64
- Wang Y H, 1979. On the classification, distribution, origin and evolution of the fishes referred to the subfamily Cyprininae of China, with description of a new species. *Acta Hydrobiol Sin*, 6: 419–438
- Yang L, Mayden R L, Sado T et al., 2010. Molecular phylogeny of the fishes traditionally referred to Cyprinini *sensu stricto* (Teleostei: Cypriniformes). *Zool Scr*, 39: 527–550
- Yasuno T, 1986. Paleontological studies of the fossil cyprinids from the late Cenozoic deposits in Japan. *Bull Seni High Sch, Fukui Prefect*, 4: 61–82
- Yasuno T, 2003. Early Miocene pharyngeal teeth (Cyprinidae) fossils from northwestern Shan-in and Kyusu, Japan (I). *Bull Fukui City Mus Nat Hist*, 50: 1–8
- Zhou W, Chu X L, 1986. Systematic study of the genus *Cyprinus* (Pisces: Cyprinidae) in Yunnan, China. *Zool Res*, 7: 297–310